

FLORAL STRUCTURE AND RELATIONSHIPS OF THE  
TRIMENIACEAE (LAURALES)

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THE FAMILY Trimeniaceae is a small western Pacific group of the Laurales, formerly included in the Monimiaceae but separated as an independent family by Gibbs (1917) and, with a detailed discussion, by Money, Bailey, and Swamy (1950). It comprises two genera, *Trimenia* Seem. (three to seven species) and *Piptocalyx* Oliver (two species) (Perkins, 1925; Rodenburg, 1971; Smith, 1978), occurring in eastern Australia, Celebes, the Moluccas, New Guinea, New Britain, Bougainville, New Caledonia, Fiji, Samoa, and the Marquesas Islands (Perkins, 1925; Rodenburg, 1971; Van Balgooy, 1975).

This study, undertaken because the Trimeniaceae were poorly known and had not yet been studied comparatively, is an investigation of the floral structure of species of *Trimenia* and *Piptocalyx*. In addition, systematic relationships, both within the family and with other groups, are discussed.

## MATERIAL AND METHODS

Floral material fixed in FAA was studied from the following species and collections:

*Trimenia papuana* Ridley

Endress 4066 (cited in the text as *E* 4066), Aug. 1977, eastern Papua New Guinea (buds, flowers, fruits).

Endress 4087, Aug. 1977, eastern Papua New Guinea (buds).

Womersley *s.n.*, Sept. 1970, eastern Papua New Guinea (buds, flowers).

*Trimenia neocaledonica* Baker f.

McPherson 4044, Aug. 1981, New Caledonia (buds).

Endress 6315, Sept. 1981, New Caledonia (buds, flowers).

*Trimenia weinmanniifolia* Seem.

Siwatibau *s.n.*, July 1971, Fiji (buds, young fruits).

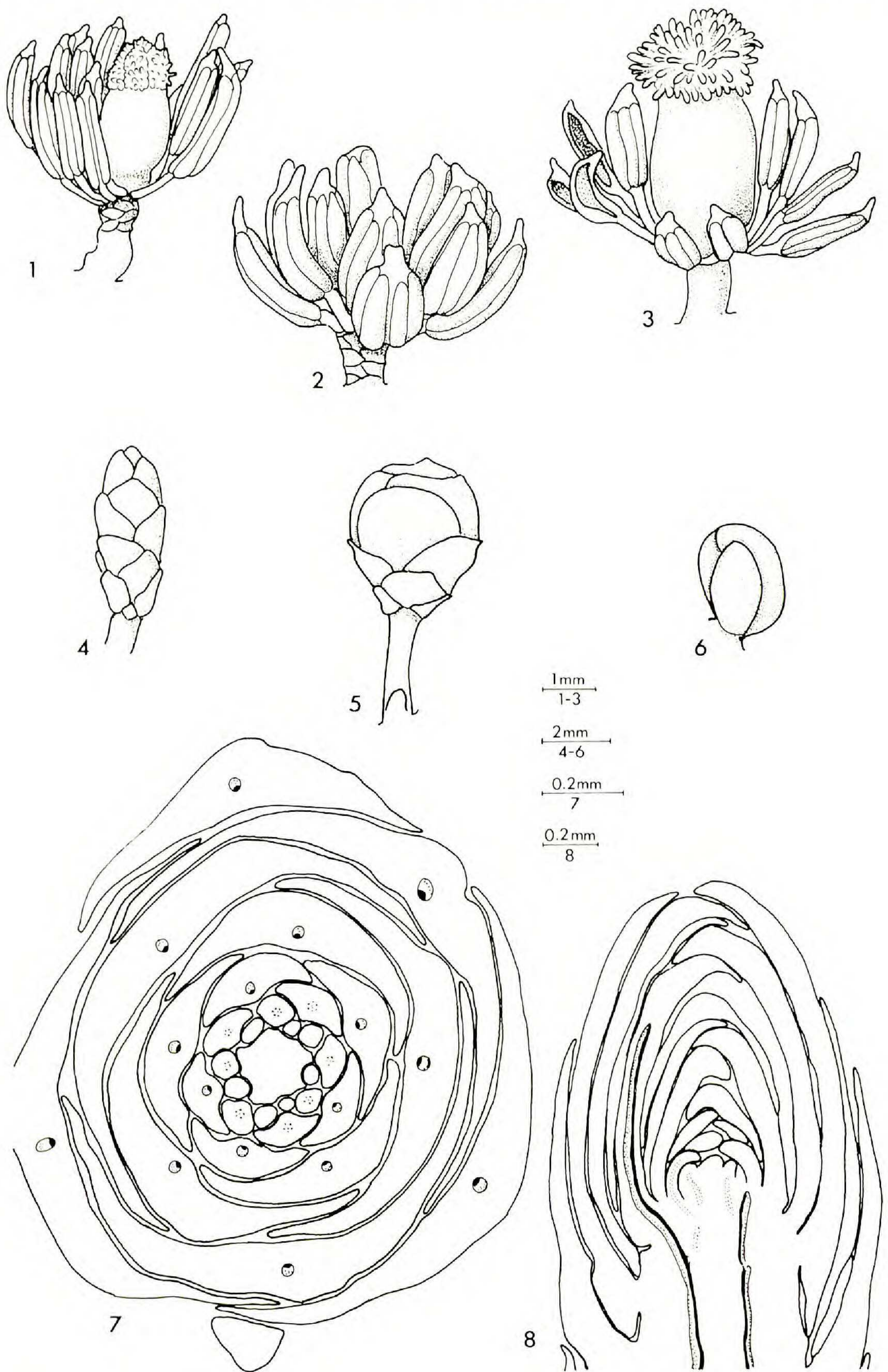
*Piptocalyx moorei* Oliver

Endress 4005, July 1977, Coffs Harbour, New South Wales, Australia (buds).

Endress 4367, Sept. 1977, Coffs Harbour, New South Wales, Australia (buds, flowers).

WELTU 13764 (*Sampson*), Aug. 1981, near Armidale, New South Wales, Australia (buds).

Plants of *Trimenia papuana*, *T. neocaledonica*, and *Piptocalyx moorei* were observed at anthesis in the field. Anatomical investigations were carried out



FIGURES 1-8. Flowers and buds. 1-3, flowers at anthesis: 1, *Trimenia papuana* (E 4066), hermaphroditic; 2, *T. neocaledonica* (E 6315), staminate; 3, *Piptocalyx moorei* (E 4367), hermaphroditic. 4-6, mature flower buds: 4, *T. papuana* (E 4066); 5, *T.*

with serial microtome sections stained with safranin and astra-blue or with Heidenhain's hematoxylin. In addition, pollen formation and development were studied by means of squashes made in iron aceto-carmin. Gynoecial structure and development were examined with the aid of a Philips 505 SEM at Victoria University of Wellington, New Zealand.

## OBSERVATIONS

### THE FLOWERS AT ANTHESIS

TRIMENIA PAPUANA. *Trimenia papuana* is a tree of tropical mountain forests. The paniculate inflorescences are produced in leaf axils and at the end of leafy shoots. They consist of many small, inconspicuous, scentless flowers. In our collections most flowers were hermaphroditic, but a few were staminate, with the gynoecium reduced or lacking. Whitish stamens with long, narrow anthers surround a normally single styleless carpel consisting of a green ovary and a terminal, tuftlike, white, dry stigma (FIGURE 1). The pollen is dry and is easily blown from open anthers. No nectar is produced. Flower visitors were not seen. These features give the impression that wind plays a major role in pollination. A peculiar feature is that before anthesis the outermost tepals fall off, and at full anthesis all the inconspicuous, brownish tepals have been shed.

OTHER SPECIES. The flowers of *Trimenia neocaledonica* (a tree) and *Piptocalyx moorei* (a vine), both occurring in subtropical rain forests, do not differ from those of *T. papuana* in the features described above (FIGURES 2, 3, 35).<sup>1</sup> Although the flowers have broader anthers and are thus slightly more showy, they too are probably predominantly wind pollinated. A difference is that in both of these species the inflorescences are fewer-flowered botryoids (racemelike panicles; for terminology see Troll, 1964). Both species are andromonoecious, with more male flowers than are present in *T. papuana*.

### PHYLLOTAXY AND NUMBER OF FLORAL PARTS

TRIMENIA PAPUANA. Phyllotaxy was determined in four flowers (two from each of two collections). The mean divergence angles of all floral parts were 137.6° and 138.7° in specimen *E 4087*, and 138.2° and 138.4° in *W*, 1970. The average of all 136 divergence angles present in the four flowers was 138.2°. The most

<sup>1</sup>Figures of inflorescences, flowers, or fruits of all species as proposed by Rodenburg (1971) have been published, some of them in remote places. Therefore, it seems reasonable to add the following iconography here: *Trimenia neocaledonica* (Rendle, Baker, & Moore, 1921; Morat & MacKee, 1977), *T. papuana* (Gilg & Schlechter, 1917; Brown, 1935; Kanehira & Hatusima, 1942; Money, Bailey, & Swamy, 1950; Smith, 1978), *T. weinmanniifolia* (Seemann, 1871; Perkins & Gilg, 1901; Hutchinson, 1973; Smith, 1978, 1981), *Piptocalyx moorei* (Maiden & Baker, 1895; Oliver, 1895; Perkins, 1911; Beadle, 1972), and *P. macrurus* (Gilg & Schlechter, 1917, 1923).

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*neocaledonica* (*M 4044*); 6, *P. moorei* (*W 13764*). 7, 8, *T. papuana* (*E 4087*), sections of flower bud at time of initiation of inner stamens: 7, transverse; 8, longitudinal (dotted areas, procambium, with phloem in differentiated vascular bundles; black areas, xylem).

regular values were obtained from flower buds in which the innermost floral parts had just been initiated.

The phyllotaxy of the flowers is spiral, with more or less constant divergence angles approaching the "limiting divergence" ( $137.5^\circ$ ) of the Fibonacci series (FIGURES 7, 41, 42). The constancy is also maintained at the transition from the perianth to the androecium and that from the androecium to the unicarpellate gynoecium (FIGURE 53). In terminal flowers the outermost "tepals" (ca. 6) are often arranged in decussate pairs before the spiral phyllotaxy starts, thus continuing the decussate phyllotaxy of the bracts on the inflorescence axis. We call them tepals because there is no abrupt change between these organs in phyllotaxy, shape, or internode length. In lateral flowers the first two phyllomes take the position of prophylls. They are situated transversely, with a somewhat larger angle to the anterior than to the posterior. It is also useful to call these organs tepals because they are not distinctive in shape or internode length from the following ones (tepals).

Thirty flowers (ten from each of three collections) revealed the following range in the number of floral parts: perianth (P), (13 to) 17 to 25 (to 28); androecium (A), 14 to 25; and gynoecium (G) (0 or) 1 (or 2). Thus, the range given by Rodenburg (1971) is extended by our collections. This result reemphasizes the wide range of variation in number of floral parts in flowers with a spiral phyllotaxy.

Because the stamens have a narrow base, they can be distinguished from tepals even at early stages in development, in spite of the unaltered phyllotaxy and similar marked plastochrons (FIGURES 7, 41). Toward the end of androecium initiation, the roundish floral apex decreases in size and becomes more or less five-angled in outline due to the effect of the adjoining stamens (FIGURE 53).

OTHER SPECIES. In *Trimenia weinmanniifolia* and *Piptocalyx moorei* the floral phyllotaxy is the same as in *T. papuana*. The flowers of these species are spirally arranged, with the mean divergence angle approaching  $137.5^\circ$ . Divergence angles were not measured in *T. neocaledonica* because young enough buds were not available, but the arrangement is clearly spiral. *Trimenia neocaledonica* differs from *T. papuana* and *P. moorei* in often having the first two (transverse) phyllomes at some distance from the flower at the base of the pedicel (FIGURES 4-6). (Such flowers were not included in the count of organ numbers.) Thus, the limits between "prophylls" and "tepals" are not clear-cut in this group.

The range in number of floral organs in the three species (from twenty flowers of each) is:

<i>Trimenia weinmanniifolia</i> (S, 1971)		
P, 14 to 23	A, 7 to 12	G, 0 or 1
<i>T. neocaledonica</i> (M 4044)		
P, 15 to 21	A, 11 to 15	G, 0 or 1
<i>Piptocalyx moorei</i> (E 4005, W 13764)		
P, 2 to 11	A, 7 to 16	G, 0 or 1 (or 2)

## PERIANTH

TRIMENIA PAPUANA. The 13 to 28 tepals gradually change in size and shape from the smaller, roundish or depressed-obovate outermost ones to the larger, obovate to spatulate inner ones (FIGURES 9, 33). The spatulate tepals form hoods over the androecium by virtue of their apically broadened and curved flanks (FIGURE 9, nos. 11–14). The outermost tepals have thick bases, with a basal extension resembling a hypopeltate bract on the dorsal side (FIGURES 8; 9, nos. 1–9; 39; 40; cf. Endress, 1975). Small-celled abscission tissue is differentiated at the base of each tepal (FIGURE 40). Abscission of a tepal starts adaxially. Toward the center of the flower the tepals become thinner, and marginal parts may be reduced to a single cell in thickness. All tepals have a single unbranched vein. The outer tepals bear uniseriate, tricellular hairs on the margins that are exposed in the bud. Each hair has an elongated apical cell. The inner tepals are glabrous.

OTHER SPECIES. In *Trimenia weinmanniifolia* the 14 to 23 tepals do not differ from those of *T. papuana* described above.

In *Trimenia neocaledonica* all 15 to 21 tepals are roundish. The outermost ones are much smaller than the inner. The basal extension is less marked than in *T. papuana*. The veins are unbranched in the outer tepals and laterally branched in the inner ones; the innermost tepal again has simplified vasculature (FIGURE 10). All tepals are glabrous.

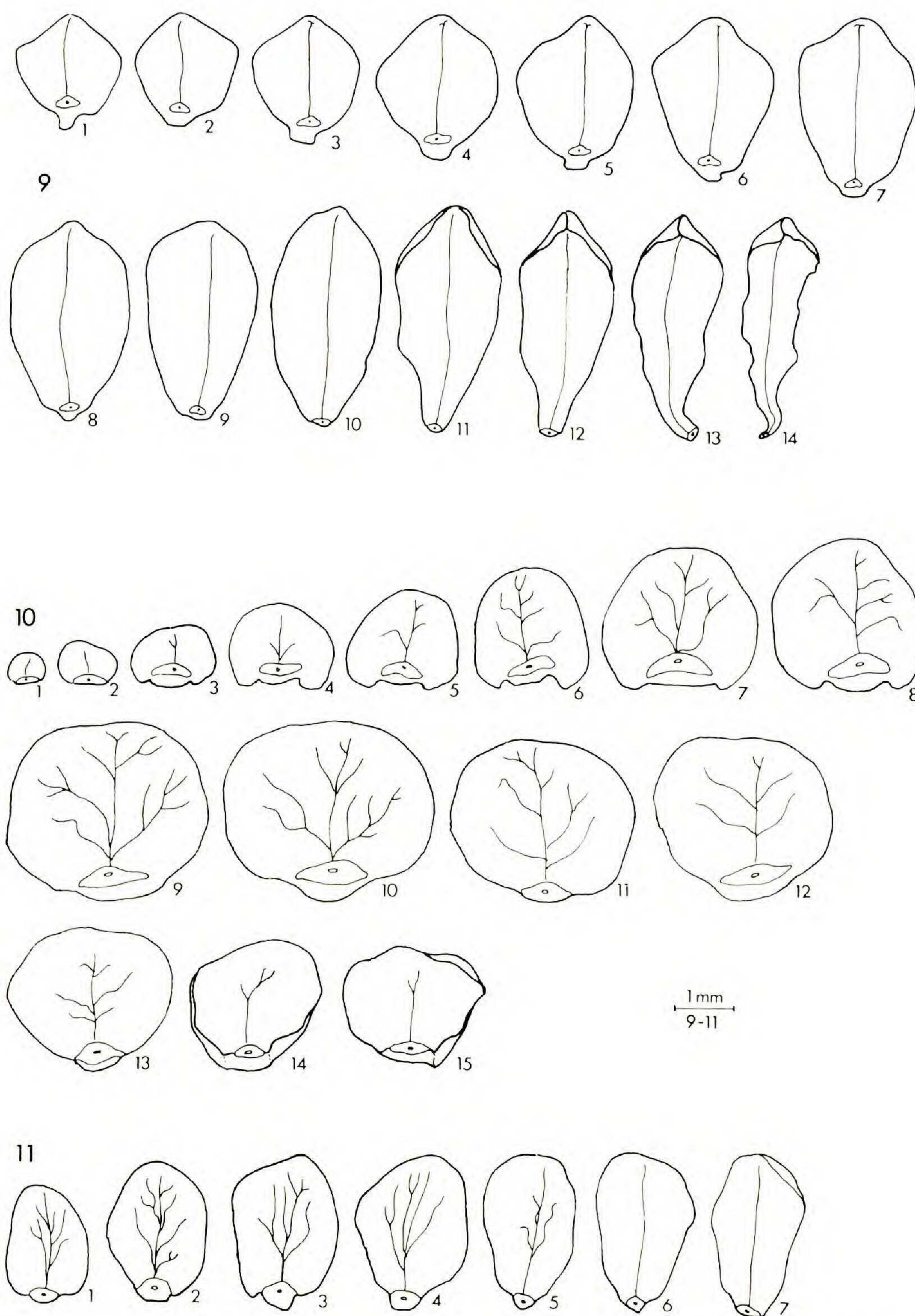
The 2 to 11 tepals of *Piptocalyx moorei* are ovate to obovate and lack a marked basal extension. The veins are branched in the outer tepals and simple in the inner ones (FIGURE 11). However, as in the other taxa, there is always only one trace to each tepal. The outer surface of the outer tepals is pilose where it has not been covered by other tepals or by the subtending bract in the young bud. The tricellular hairs resemble those of *Trimenia papuana*.

## ANDROECIUM

In *Trimenia papuana* the 14 to 25 stamens are ca. 4 mm long and slender (FIGURES 13, 14, 34). The anther and the filament are equal in length. The mature anther is latrorsely dehiscent, opening by two lateral slits (FIGURE 17). It is capped by a short, linguiform connective apex. One collateral vascular bundle serves the stamen, ending in the connective apex in a group of short, tracheidlike cells. In a few flowers transitional forms between tepals and stamens have been seen; these were spatulate organs with a rudimentary pollen sac situated toward the base (FIGURE 12).

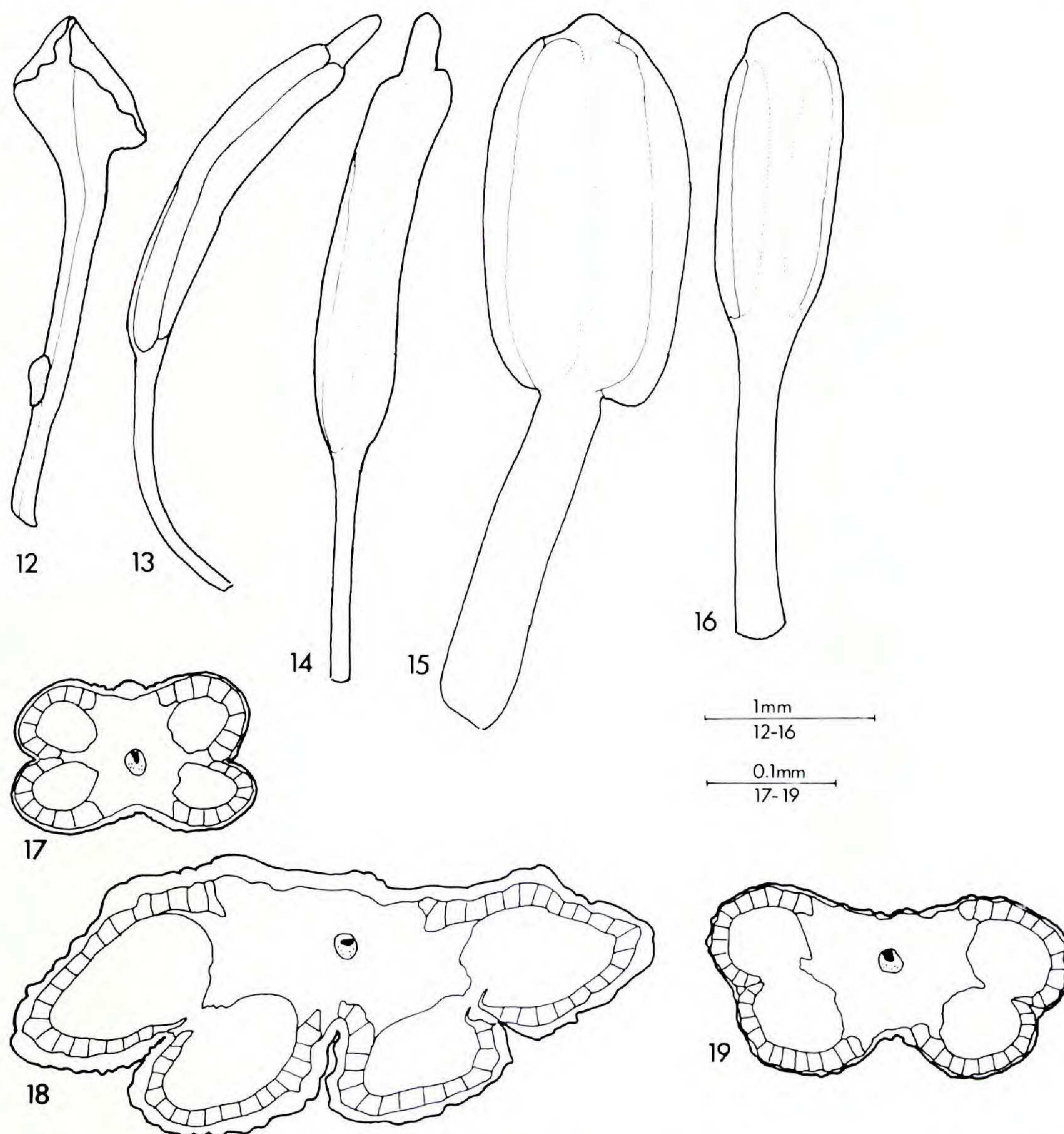
Although the 11 to 15 stamens of *Trimenia neocaledonica* and the 7 to 16 of *Piptocalyx moorei* are of about the same length as those of *T. papuana*, they have much broader filaments and broader, extrorsely dehiscent anthers (FIGURES 15, 16, 18, 19, 43). In all three species there is a considerable increase in filament length from the time tepals are detached to when pollen is shed.

The anthers are tetrasporangiate in all species. Both genera have microsporangia with large, persistent epidermal cells (smallest in *Trimenia papuana*, largest in *T. neocaledonica*) and an endothecium that develops the characteristic



FIGURES 9-11. Tepals of mature flower buds (each sequence from one bud), adaxial view: 9, *Trimenia papuana* (E 4066), outermost tepals not drawn; 10, *T. neocaledonica* (E 6315); 11, *Piptocalyx moorei* (E 4367).

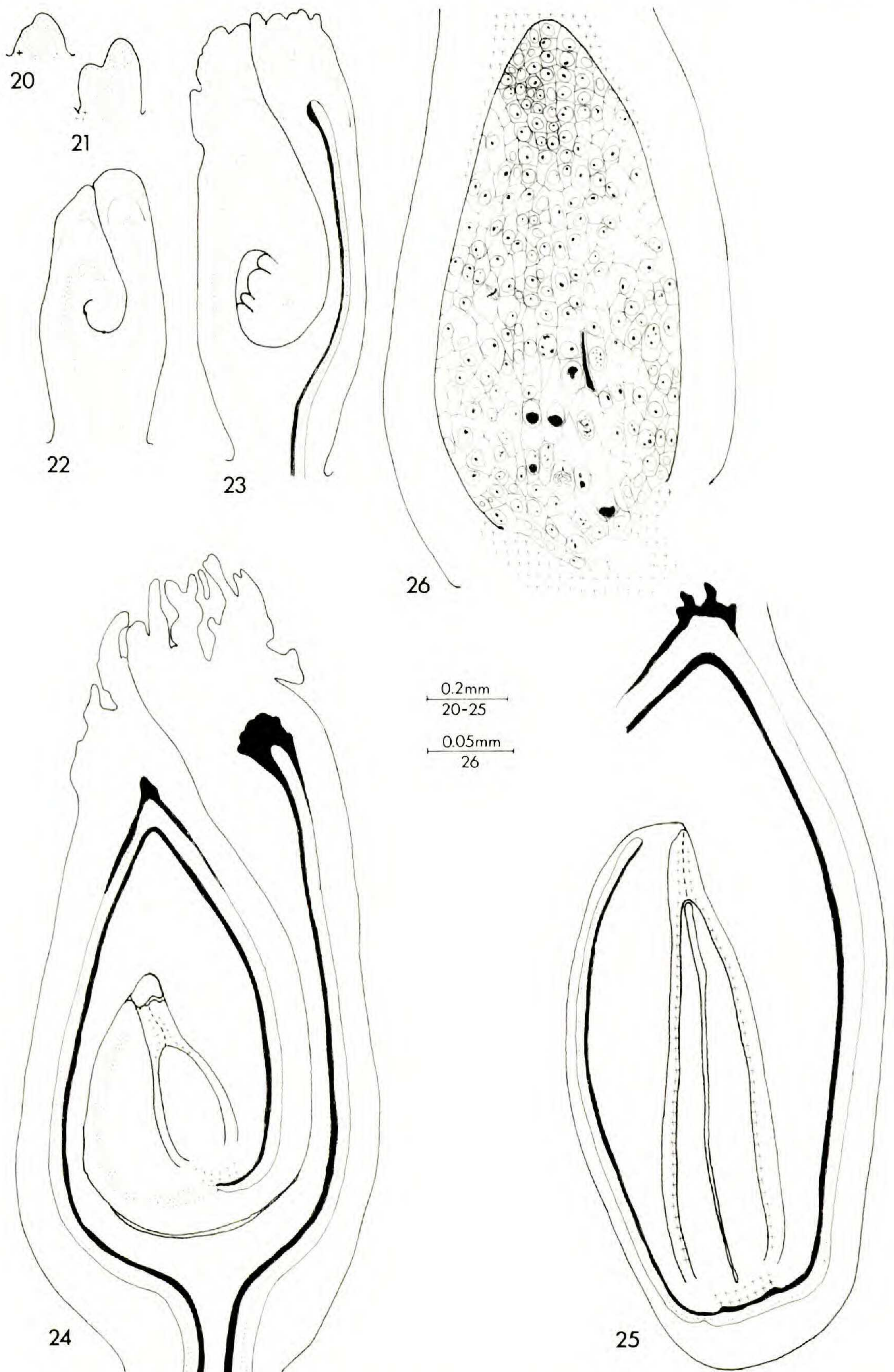
fibrous radial bars of thickening. The endothecium is restricted to the external part of each theca and is absent in the connective (FIGURE 43), which has a high tannin content. There is an irregularly one- or two-layered middle wall region that becomes crushed before anthesis. FIGURE 44 illustrates a stage in



FIGURES 12-19. Stamens. 12, *Trimenia papuana* (E 4066), innermost tepal with rudimentary pollen sac, adaxial view, from mature bud. 13, *T. papuana* (E 4066), stamen at anthesis, lateral view (right side = adaxial). 14-16, stamens at anthesis, abaxial view: 14, *T. papuana* (E 4066); 15, *T. neocaledonica* (E 6315); 16, *Piptocalyx moorei* (E 4367). 17-19, anthers shortly before dehiscence, transverse sections, adaxial side above, endothecium hatched: 17, *T. papuana* (E 4066); 18, *T. neocaledonica* (E 6315); 19, *P. moorei* (E 4367).

the development of the microsporangium of *Piptocalyx moorei* after the epidermis, endothecium, and middle wall layer have been differentiated. A single-layered tapetum encloses sporogenous tissue that is still undergoing cell division (not visible in the photograph).

The tapetum is glandular, and by the time pollen mother cells have reached the early stages in prophase I of meiosis, most tapetal cells are binucleate (*Trimenia papuana*, *Piptocalyx moorei*). Microsporogenesis was observed in *T. papuana*. Cytokinesis is of the successive type, with wall formation by a centrifugal cell plate occurring at the end of meiosis I and II (FIGURES 45, 46).



FIGURES 20-26. *Trimenia papuana*, carpel development, median longitudinal sections (left side = adaxial): 20, origin of ventral "cross zone" (E 4087); 21, chairlike stage (W, 1970); 22, early epidermal periclinal divisions in future stigmatic region (cell rows



The resulting tetrads are isobilateral, decussate, or intermediate between these types. In the limited material examined (several buds from a single collection), division stages were synchronized in each microsporangium throughout meiosis—an unusual feature. Although early stages in the division of pollen mother cells are normally synchronous due to linkage by cytoplasmic channels, exact synchronicity is usually subsequently lost when a callose wall forms around each meiocyte (Heslop-Harrison, 1966). Individual microspores within a tetrad are bilaterally symmetrical (FIGURE 47). Due to dissolution of callose wall material, microspores have a plano-convex shape for a time after they have separated; this reveals their orientation when they are in tetrads. Thus in FIGURE 48 the center of the curved edge of the microspore is at the distal pole. With maturation the pollen grains of *T. papuana* become more rounded, but they retain an ellipsoid (rather than spherical) shape. When pollen mitosis occurs, the generative cell is cut off so that it lies midway between the two more pointed ends of the grain. This is also the case in *T. neocaledonica* (FIGURE 49) and *P. moorei*. In these two species pollen is biaperturate, with the centers of the apertures located at the two more pointed ends of each grain. This is in contrast to *T. papuana*, which in our collections had inaperturate pollen (Sampson & Endress, in press). Polyforate pollen has been reported in some collections of this species (Walker, 1976) and in *T. weinmanniifolia* (Money, Bailey, & Swamy, 1950). Although our material of *T. neocaledonica* and *P. moorei* did not contain stages with pollen in tetrads, we assume (by analogy with *T. papuana*) that the more pointed ends of the grains are equatorially aligned and therefore that the pollen is disulculate (in the terminology of Walker, 1976). Because the nascent generative cell is equidistant from the two apertures, it obeys Huynh's "law of the longest distance" (Huynh, 1972; Sampson, 1982). The generative cell is soon detached from the wall of the grain to lie within the cytoplasm of the generative cell. In all three taxa the pollen is shed in the two-celled stage (FIGURES 50, 51).

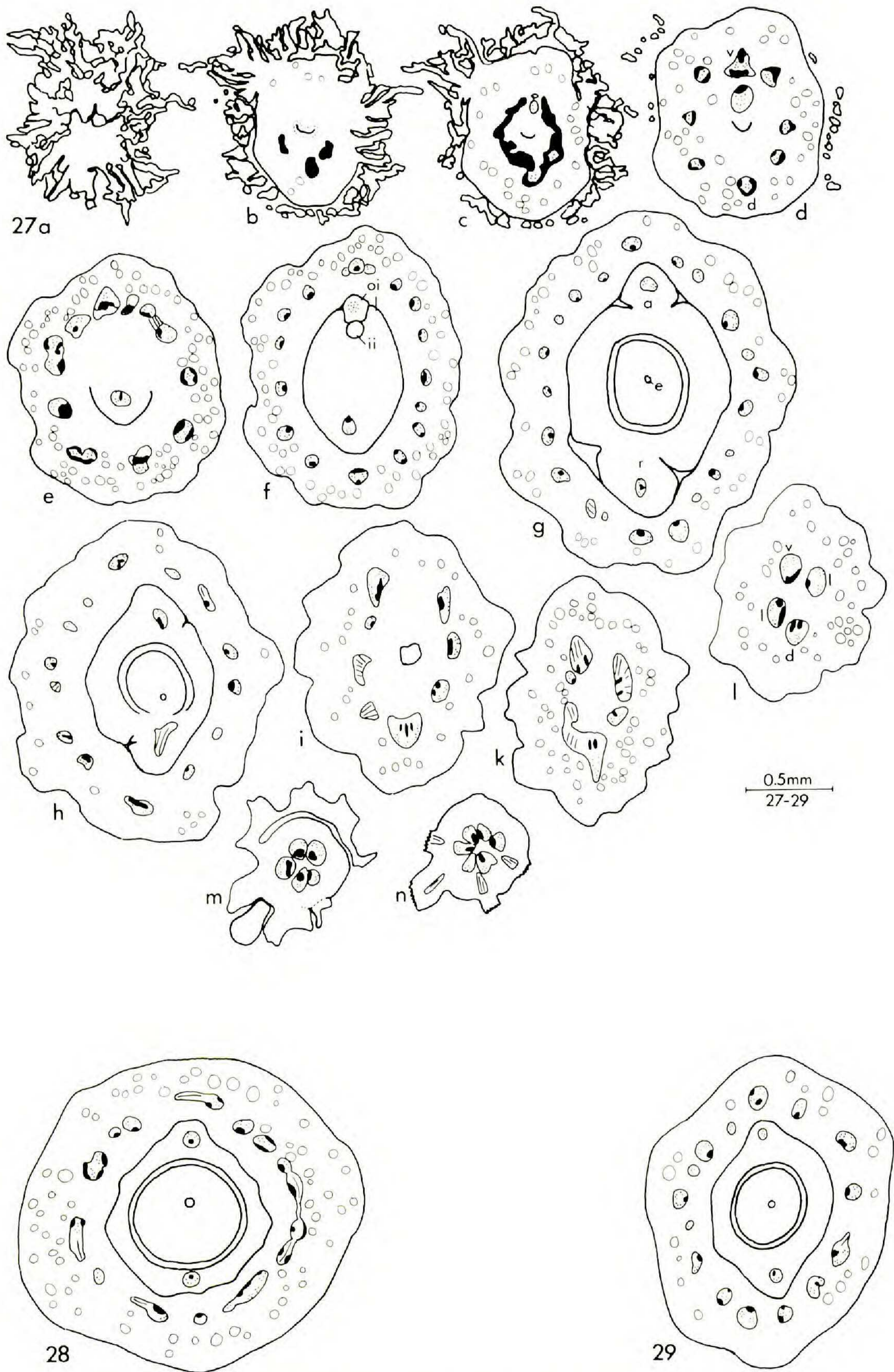
The septum between each pair of microsporangia breaks down before dehiscence (FIGURE 43). Lateral longitudinal slits are formed, each by separation of small cells along a line of weakness (stomium) at the outermost part of the wall that separates radially adjacent microsporangia, and pollen is shed.

#### GYNOECIUM

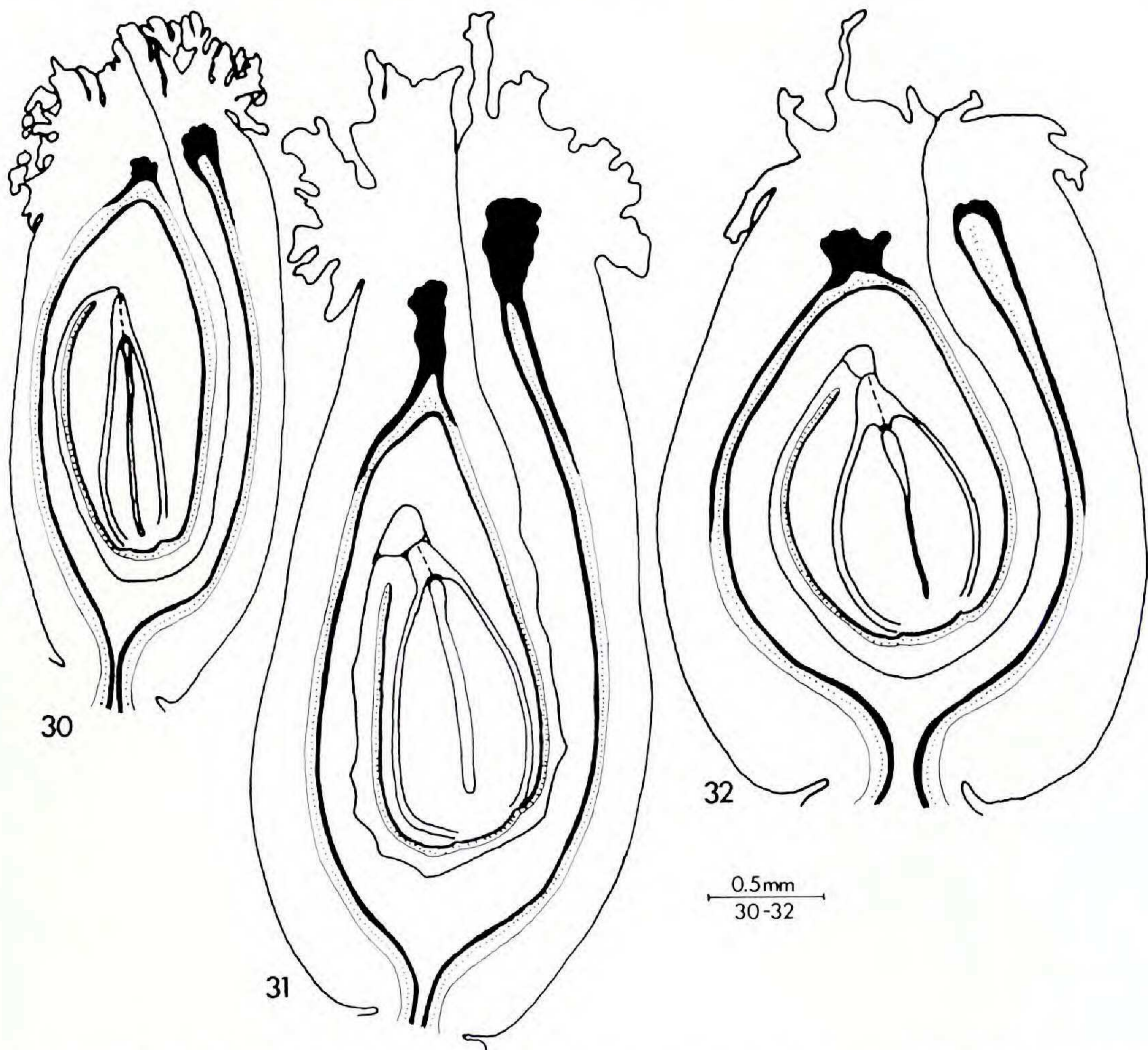
TRIMENIA PAPUANA. The gynoecium consists of one (very rarely two) carpels. At anthesis the carpel is ca. 2 mm long and 1 mm broad. The barrel-shaped,

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of epidermal origin indicated), inception of inner integument (*E* 4087); 23, rotation of ovule almost completed, ventral vascular bundle still procambial (*E* 4087); 24, stage with meiocytes in ovule, integumentary vascular bundle still procambial (cf. FIGURE 26) (*W*, 1970); 25, ovule at anthesis, elongated nucellus and long, tubular embryo sac (*W*, 1970); 26, nucellus with numerous meiocytes (enlarged from FIGURE 24) (*W*, 1970). (Dotted areas: meristematic tissue; procambium; phloem in differentiated vascular bundles. Black areas: xylem in differentiated vascular bundles. Plus signs: tanniferous tissue. Black lines in stigmatic region: cell rows.)



FIGURES 27-29. Transverse sections of carpels at anthesis (adaxial side up). 27, *Trienia papuana* (E 4066), series from 1 carpel: a, stigma, "cross zone"; b, upper extension of dorsal bundle and 2 adjacent bundles; c, vascular bundles forming ring; d, e, top of

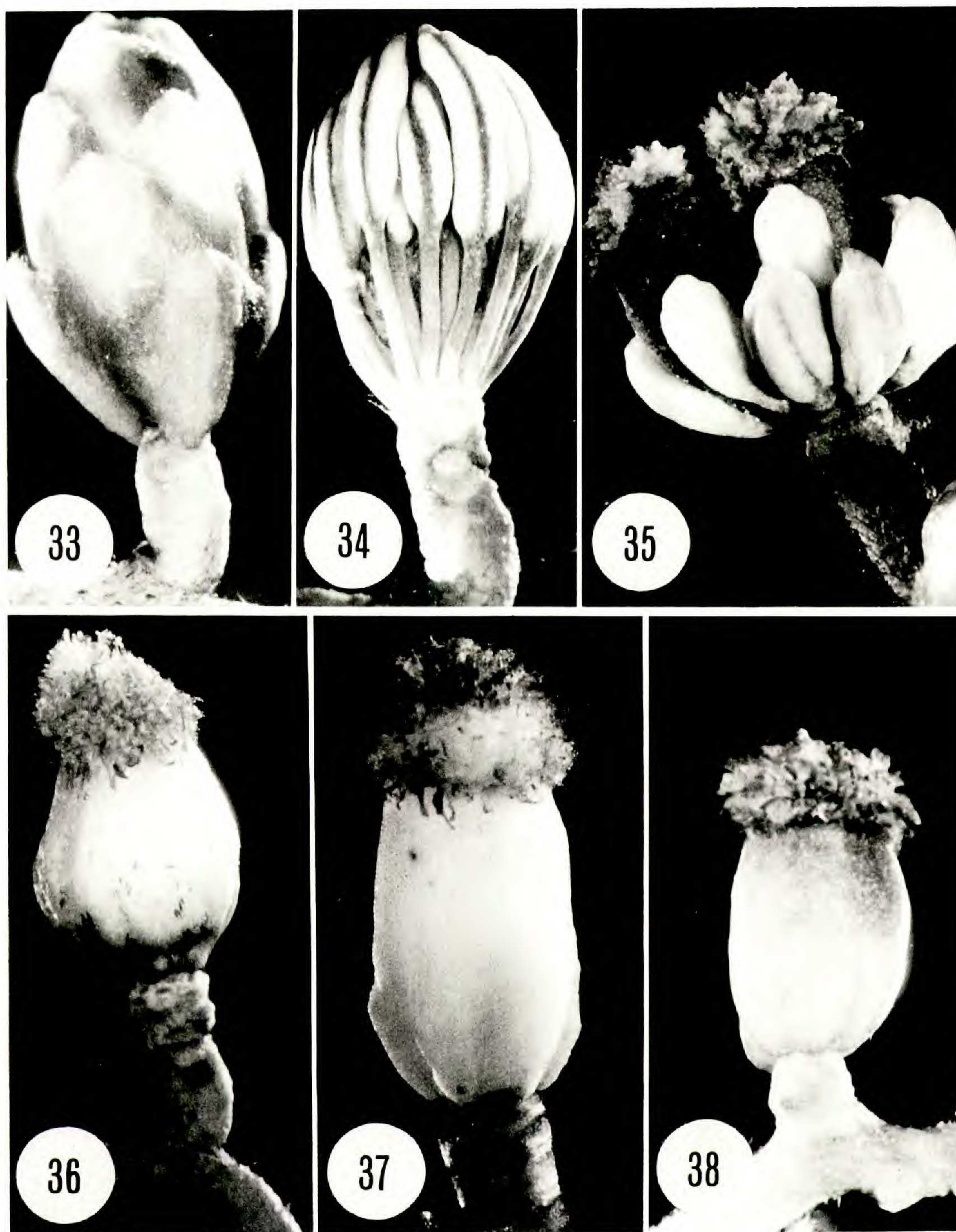


FIGURES 30–32. Median longitudinal sections of carpels at anthesis (left side = adaxial): 30, *Trimenia papuana* (W, 1970); 31, *T. neocaledonica* (E 6315); 32, *Piptocalyx moorei* (E 4367). (Dotted areas: phloem. Black areas: xylem.)

slightly asymmetric ovary is topped by a capitate, tuftlike stigma; there is no distinct style (FIGURES 1, 36, 63). The carpel is remarkable in being extremely utriculate (FIGURE 30). At anthesis the ventral and dorsal regions are nearly the same length. The ventral “cross zone” is situated at the top of the carpel in the stigmatic region (FIGURE 30). The “stylar” canal remains a narrow, transverse slit resulting from thickening but not widening of the carpellary wall (FIGURE 27, a–d). Longitudinal shallow furrows on the ovary surface mark the position of the anthers in bud. On the ridges between these depressions, rows

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ovary; f, tip of outer (oi) and inner (ii) integuments; g, middle region of ovary (raphe (r) and antiraphe (a) separated from central body of ovule by deep furrows; embryo sac (e)); h, base of nucellus and integuments; i, base of ovarian cavity; k, l, union of vascular bundles into 1 dorsal (d), 1 ventral (v), and 2 laterals (l); m, base of ovary, rearrangement of carpellary bundles toward stele; n, level of androecium, stele with stamen traces. 28, *T. neocaledonica* (E 6315), middle region of ovary. 29, *Piptocalyx moorei* (E 4367), middle region of ovary, slightly earlier stage. (Dotted areas: phloem. Black areas: xylem. Small circles at periphery of sections: mucilage cells.)



FIGURES 33–38. Bud, flowers, and gynoecia,  $\times 10$ . 33, *Trimenia papuana* (E 4066), mature bud, outermost tepals fallen. 34, *T. papuana* (E 4066), flower shortly before anthesis, tepals removed. 35, *Piptocalyx moorei* (E 4367), bicarpellate flower at early anthesis. 36–38, gynoecia after anthesis: 36, *T. papuana* (E 4066); 37, *T. neocaledonica* (E 6315); 38, *P. moorei* (E 4367).

of hooklike, upwardly directed, unicellular hairs are developed (FIGURES 60, 61). The carpel contains one ovule in a ventral-median position. The ovule is crassinucellar, bitegmic, anatropous, and pendent, with the micropyle directed upward (FIGURES 25, 27, 30, 64).

At anthesis a number of branching and anastomosing bundles (up to ten on each side) extend through the ovary wall between the dorsal and the ventral vascular bundles (FIGURE 27, g). They are more numerous than as described by Money, Bailey, and Swamy (1950, *table 3*, p. 389)—20 or more compared to four or five! The dorsal bundle terminates immediately below the stigma, and the other bundles are slightly shorter (FIGURE 27, b). The bundles all join near the top, forming a ring of short, tracheidlike cells (FIGURE 27, c). In the upper region of the carpel, each bundle has several tracheids on its outer side, while the normal xylem on the inner side is smaller (FIGURES 27, d; 30). Toward the base of the carpel, the lateral bundles anastomose, so that four more or less clear-cut complex bundles remain: a dorsal, a ventral, and two laterals (FIGURE 27, h–m). There is no obvious reorientation of the bundles demarcating the transition between the gynoecium and the floral stele, in contrast to the situation in many other plants.

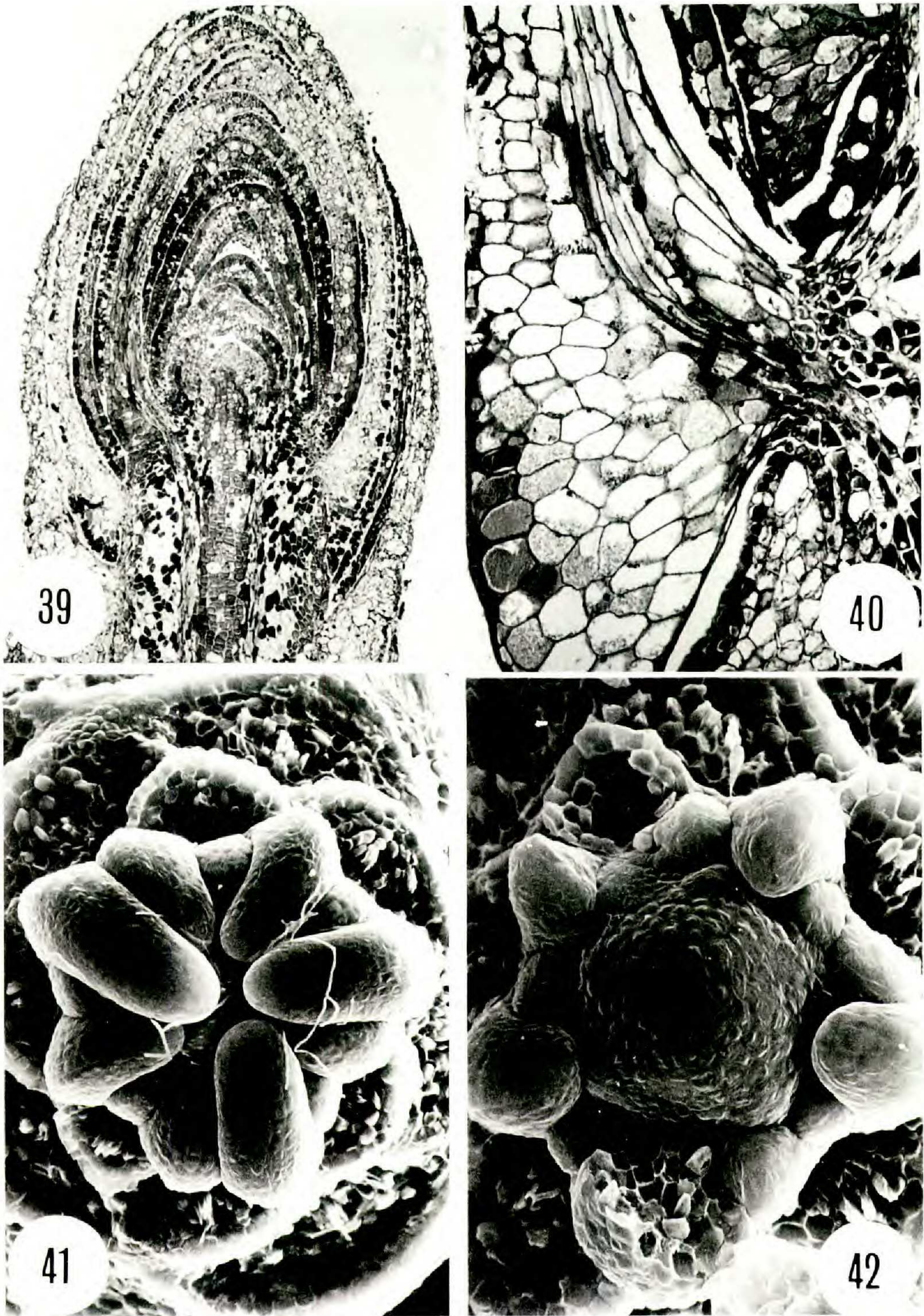
A strand from the ventral bundle supplies the ovule. The ovular bundle does not terminate at the chalaza but extends to the top of the outer integument near the micropyle (FIGURES 25, 27). Here, the outer integument has a very short, discrete tip (FIGURE 27, f). In the raphe and the outer integument (antiraphe) the vascular bundle occupies the peripheral region, which suggests that thickening of these parts occurs only on their inner side.

The inner integument is three or four cells thick. The outer integument is about six or seven cells thick, except at the top (ten to fifteen cells) and in the vascularized median region. There are three histologically conspicuous cell layers: the very small celled, “meristematic” inner epidermis of the ovary wall; the outer epidermis of the outer integument, with radially much elongated cells that develop into the stony layer of the seed; and the inner epidermis of the inner integument, which is tanniferous (FIGURE 25).

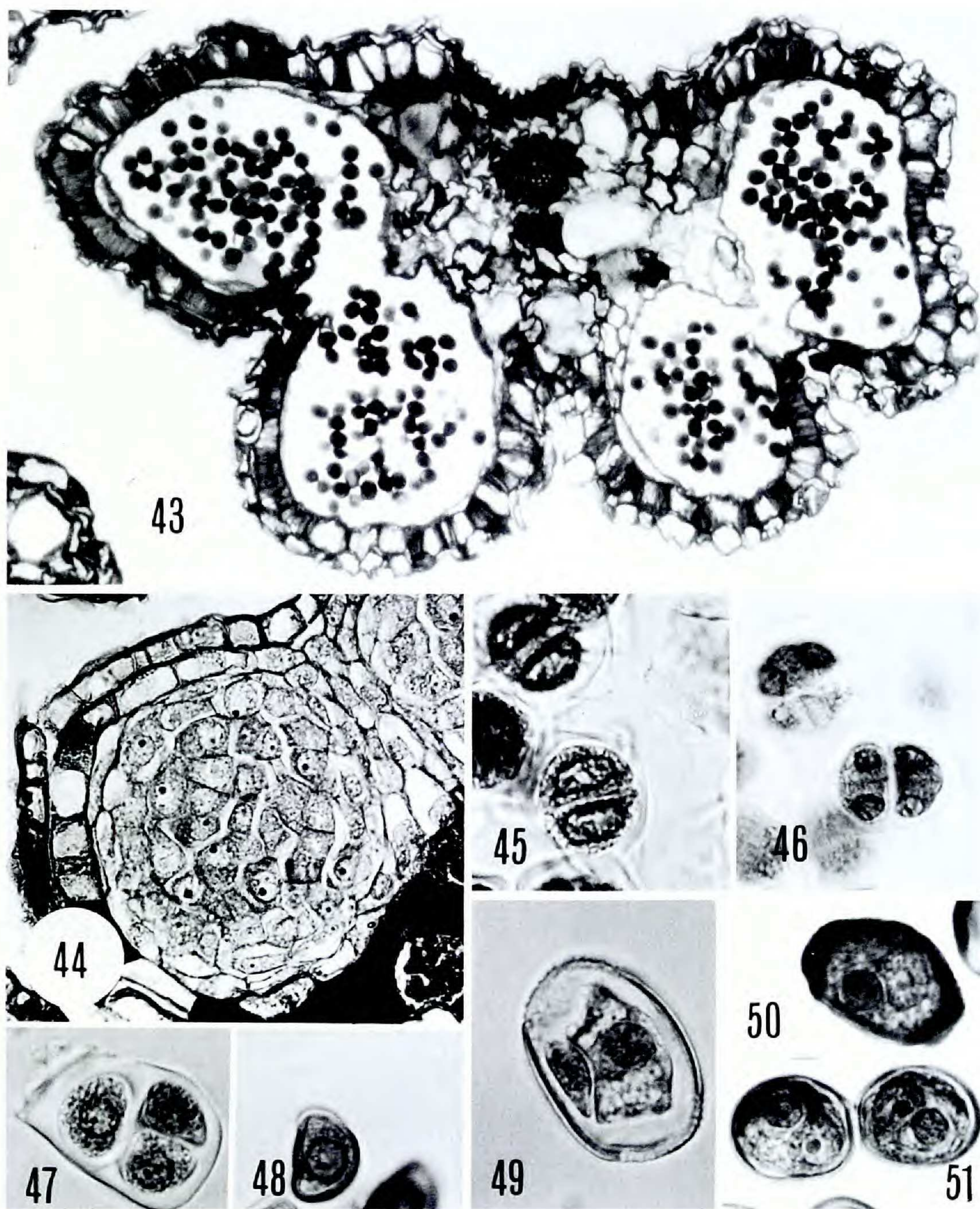
The ovule almost completely fills the ovary; the small gaps in between contain a mucilaginous secretion. In the middle region of the ovary, deep furrows separate the raphe and the antiraphe from the central portion of the ovule (FIGURE 27, g, h). The inner integument forms a massive cap over the micropyle, with the center containing a tanniferous zone (FIGURES 25, 64). The outer integument is also involved in micropyle formation. The long, narrow embryo sac extends throughout the entire length of the nucellus, almost growing out of the top of it (FIGURE 25).

The plumose stigma consists of long, pluricellular, pluriseriate, tanniferous hairs (FIGURE 62). The periphery of the carpel contains numerous large mucilage cells and—in the uppermost part—some groups of weakly lignified cells; the upper part of the center of the carpel (and ovular base) has especially thick-walled (but not lignified) cells with irregular thickenings. It seems unlikely, however, that this is pollen tube transmitting tissue because the cells are isodiametric, not elongated. Pollen tubes probably grow only through the narrow “stylar” canal. Together with the ovular surface, this tissue becomes lignified, beginning in its center, during fruit development.

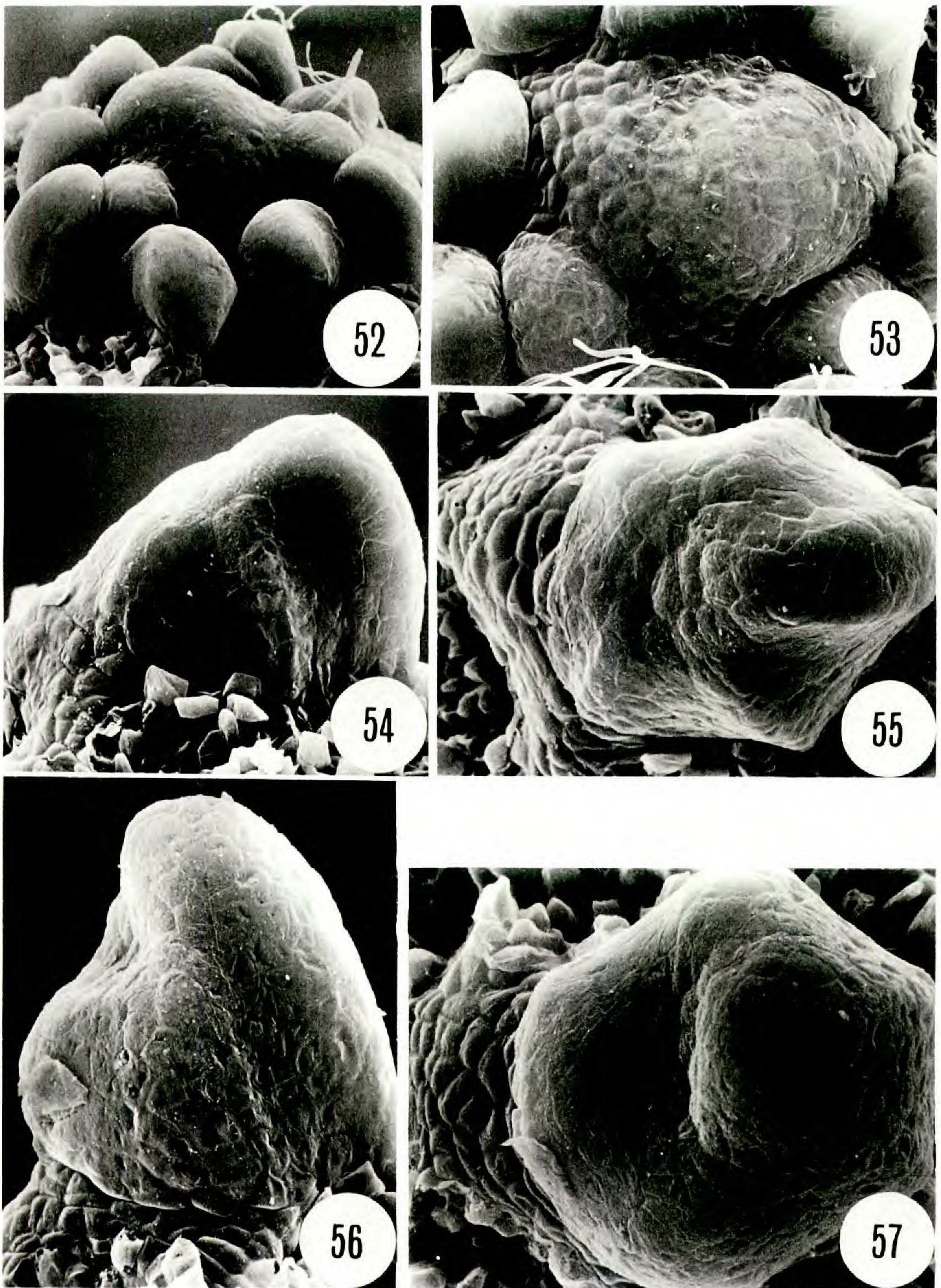
Soon after anthesis, the ovary wall interior to the vascular bundles becomes tanniferous. There is no further lignification in the ovary wall. The groups of



FIGURES 39–42. *Trimenia papuana*. 39, floral bud at time of androecium initiation (*E* 4087), median longitudinal section,  $\times 40$  (cf. FIGURE 8). 40, abscission of outer tepal from mature bud (*E* 4066), median longitudinal section (note dorsal extension),  $\times 100$ . 41, 42, floral buds at time of initiation of inner stamens (*E* 4087), note spiral phyllotaxy: 41, tepals and few outermost stamens removed,  $\times 120$ ; 42, tepals and many outer stamens removed,  $\times 200$ .



FIGURES 43-51. Anther and pollen development. 43, *Trimenia neocaledonica* (E 6315), transverse section through nearly mature anther,  $\times 100$ . 44, *Piptocalyx moorei* (E 4005), portion of transverse section through young anther, showing microsporangium with sporogenous tissue,  $\times 375$ . 45-48, *T. papuana* (W, 1970),  $\times 800$ : 45, pollen mother cells at prophase II; 46, pollen mother cells at telophase II; 47, young tetrad with callose wall material enclosing microspores (only 3 visible); 48, young microspore soon after separation from tetrad. 49, *T. neocaledonica* (M 4044), pollen grain soon after formation of vegetative cell and generative cell (at left),  $\times 800$ . 50, *P. moorei* (E 4367), mature pollen grain,  $\times 800$ . 51, *T. papuana* (E 4066), mature pollen grains,  $\times 800$ .



FIGURES 52–57. *Trimenia papuana* (E 4087). 52, 53, floral apex at time of carpel initiation: 52, lateral view,  $\times 200$ , carpel primordium at left; 53, from above,  $\times 330$ , carpel primordium at right. 54, 55, carpel primordium with ventral “cross zone” differentiated: 54, lateral view,  $\times 360$ ; 55, from above,  $\times 410$ , note residual floral apex at left with convex cell surfaces. 56, 57, carpel primordium at chairlike stage: 56, lateral view,  $\times 360$ ; 57, from above,  $\times 410$ .



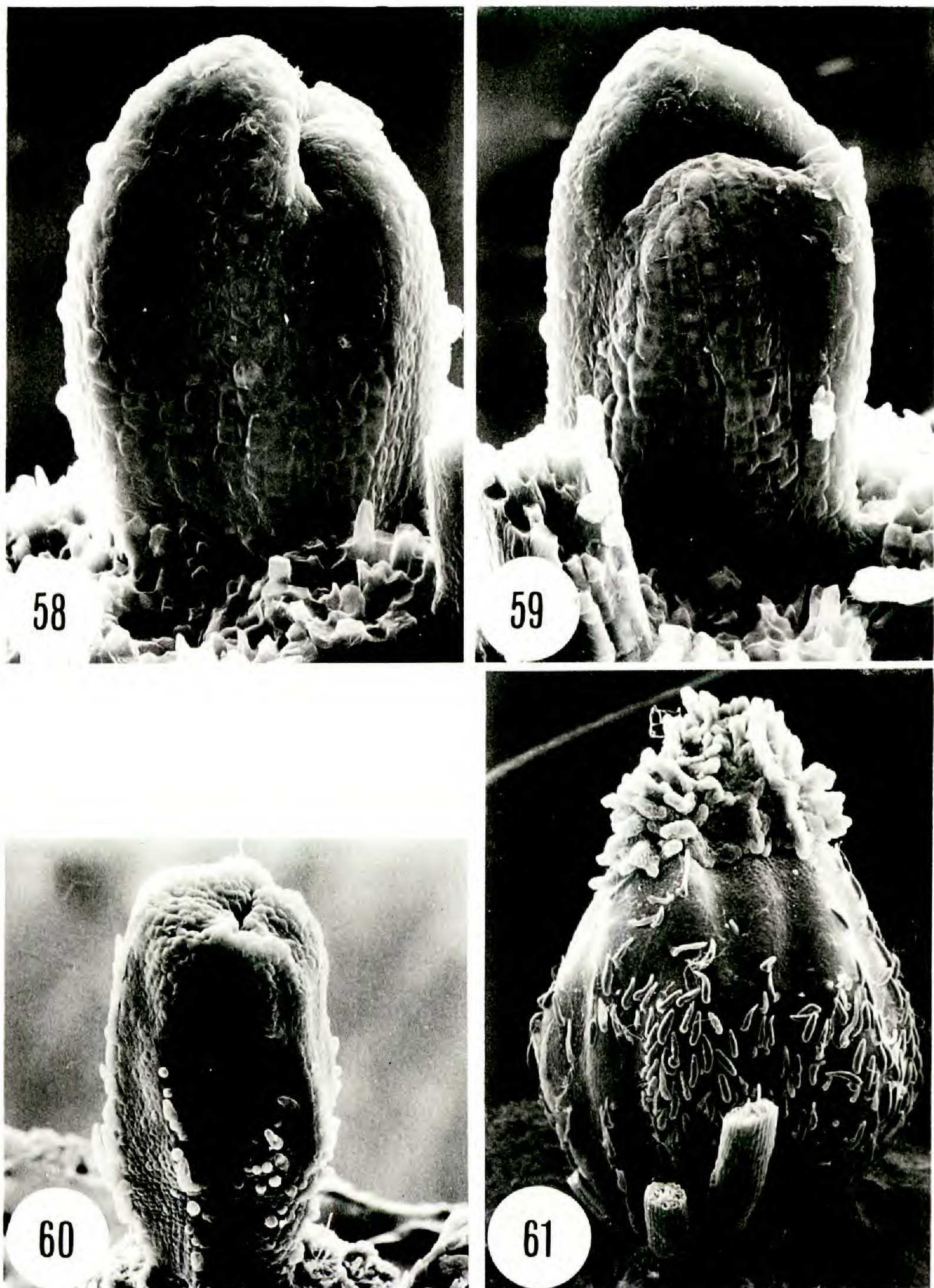
weakly lignified cells at the upper periphery of the carpel do not differentiate further.

The carpel is initiated at a normal divergence angle from the last stamen, to one side of the apex (FIGURE 53). Since a small portion of the ventral part of the apex is not used up during carpel formation, the carpel is not truly terminal. In SEM preparations the residual apex is distinguished by its convex cell surface; on the fast-growing carpel primordium the cell surface is flatter (FIGURES 52–57). Histologically, the residual apex soon becomes tanniferous (FIGURES 20, 21). The carpel primordium is thicker than a stamen primordium even at a morphologically undifferentiated stage (FIGURE 53). The carpel primordium soon becomes angled because of the protruding neighboring stamen primordia (FIGURES 55, 57). Halfway up its ventral side a platform (“cross zone”) arises (FIGURES 20, 54), and the carpel primordium becomes chair shaped (FIGURES 21, 56). At this stage the carpel bears considerable resemblance to those of the Lauraceae (Endress, 1972) and certain Monimioideae of the Monimiaceae (Sampson, 1969a; Endress, 1980a). Unlike in the Lauraceae and the Monimioideae, however, during further development by extensive intercalary elongation, the relative difference in length between dorsal and ventral parts decreases, and the carpel becomes extremely utriculate (FIGURES 22–24, 58–60). There is an early inception of the pluricellular stigmatic papillae, coupled with (and even preceded by) extensive periclinal cell divisions of the epidermis in the apical part of the carpel (FIGURES 22, 23, 60). The stigma is conical in bud; only at anthesis does it expand and become capitate (FIGURES 61, 63).

By anthesis, the ovule has rotated almost 360° from the original ventral cross zone where it originated (FIGURES 21–25, 30). The inner integument appears before the outer, as is normal in bitegmic ovules (FIGURE 22). The nucellus undergoes relatively little growth until meiosis and is soon overtopped by the inner integument. This leaves only a narrow micropyle, which becomes indistinct even before anthesis (FIGURE 24).

At the time of integument initiation, the nucellar tissue consists of relatively small cells and an archesporium is not yet distinct. Later, numerous meiocytes differentiate at the base of the nucellus (FIGURES 24, 26, 64). Thus, the archesporium is multicellular. One or several embryo sacs start growing after meiosis, but only one reaches maturity. It grows like a narrow tube toward the apex of the now fast-elongating nucellus and stops immediately at the border of the nucellar apex, near the cap over the nucellus formed by the inner integument (FIGURE 25). There it becomes more voluminous. The egg apparatus and polar nuclei are situated near the nucellar apex, while the antipodals probably remain at the base of the embryo sac tube but are hard to trace. It appears as if the tanniferous hypostase and the tanniferous cap over the nucellus formed by the inner integument prevent further elongation of the intrusive embryo sac apices at both ends of the nucellus.

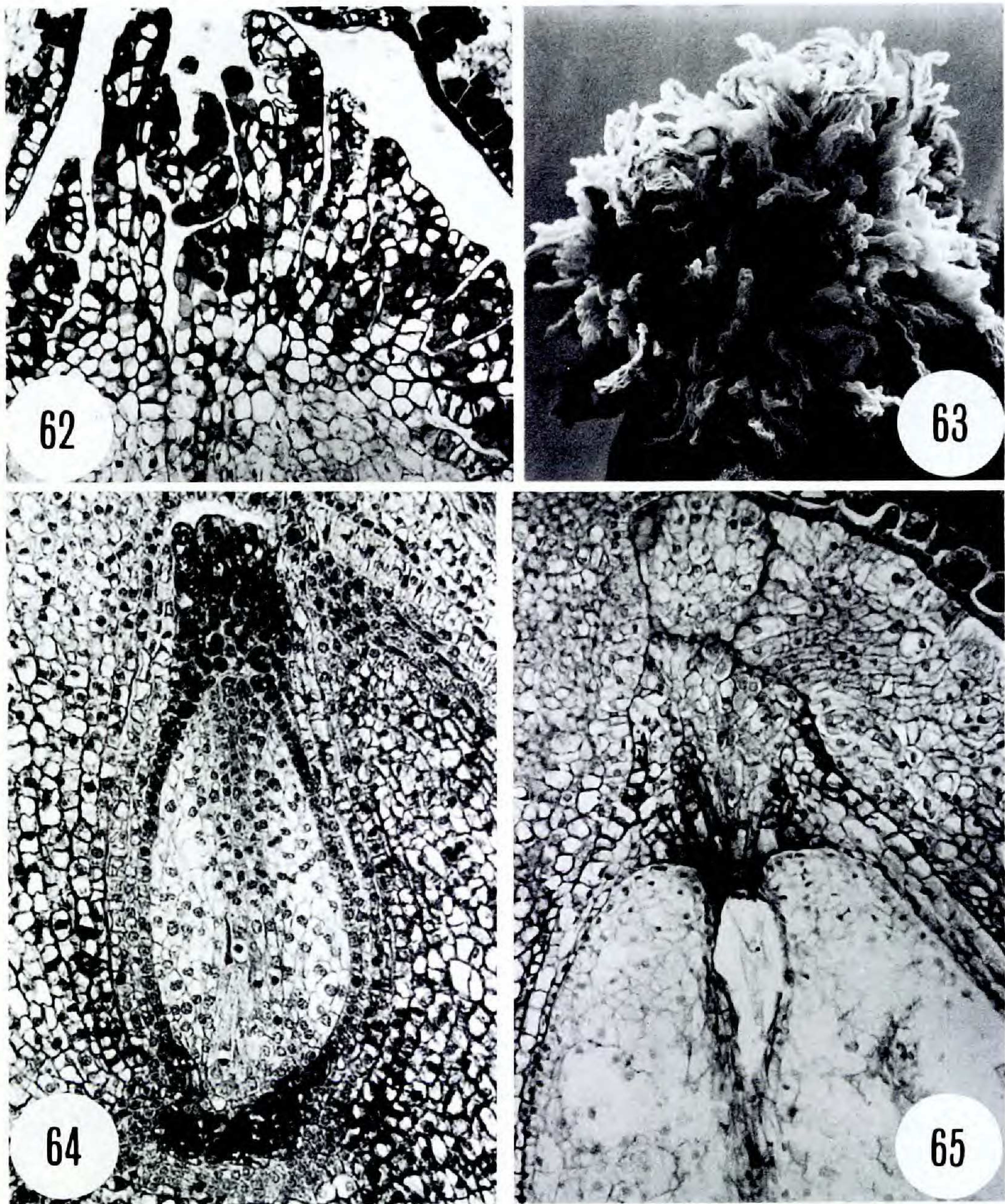
OTHER SPECIES. The gynoecial structure of *Trimenia neocaledonica* and *Piptocalyx moorei* closely resembles that of *T. papuana* (FIGURES 31, 32). Therefore, only differences will be mentioned.



FIGURES 58–61. *Trimenia papuana*. 58, 59, young carpel after intercalary longitudinal growth of middle and basal regions,  $\times 220$  (note longitudinal cell “families”): 58, lateral view; 59, from adaxial side. 60, young carpel at inception of stigma differentiation (*W*, 1970),  $\times 80$ . 61, carpel with conical stigma, from older bud (*E* 4066),  $\times 30$ .

In *Trimenia neocaledonica* the carpel at anthesis is longer (ca. 3 mm) than in *T. papuana* (FIGURES 31, 37). Histologically, the whole carpel is richer in tannins; the mucilage cells at the carpel periphery are larger, and their mucilage content seems to be higher (FIGURE 28). The ovule is thicker than in *T. papuana*.

In *Piptocalyx moorei* the carpel is ovoid and thicker (ca. 1.5–2 mm) but not



FIGURES 62–65. Stigmas and ovules. 62–64, *Trimenia papuana*: 62, stigma from old bud (*E* 4066), longitudinal section,  $\times 100$  (note pluricellular papillae); 63, stigma at anthesis (*E* 4066),  $\times 30$ ; 64, ovule with several meiocytes (*W*, 1970), median longitudinal section,  $\times 160$  (note tanniferous tissue in top of inner integument and hypostase). 65, *Piptocalyx moorei* (*E* 4367), ovule at anthesis, longitudinal section,  $\times 120$ , nucellar apex depressed and with papilla, embryo sac apex inside papilla.

longer than in *Trimenia papuana* (FIGURES 32, 38). Histologically, the tannin content is lower. There are fewer (but larger) mucilage cells (FIGURE 29). In the upper carpel wall the outer tracheid zone of the vascular bundles is even more developed than in *T. papuana*. The most obvious difference in the ovular structure at anthesis is that the nucellar apex is depressed, and in the center of this depression the tip of the ripe embryo sac is situated inside a papilla (FIGURES 32, 65). The inner integument contains conspicuously elongated cells near the

depression. In both species the ovary walls are glabrous, in contrast to those of *T. papuana*.

## DISCUSSION

### STRUCTURE OF FLORAL ORGANS

**PHYLLOTAXY, NUMBER, AND INITIATION OF FLORAL PARTS.** The floral organs have a spiral phyllotaxy in all four species examined. This has not been recognized in earlier studies. While some authors (Perkins & Gilg, 1901; Gibbs, 1917; Perkins, 1925; Rodenburg, 1971) report a spiral perianth for *Trimenia* species, only Morat and MacKee (1977) state that the androecium has a spiral phyllotaxy (in *T. neocaledonica*). The reason is that the spiral is obscured during later ontogeny because of differential expansion of the flower base caused by the extensive enlargement of the carpel. In *Piptocalyx* spiral floral phyllotaxy has not previously been recognized.

The analysis of floral parts in our material has extended the previously recorded range of variation in stamen number in all species, and in tepal number in all species except *T. weinmanniifolia* (Rodenburg, 1971; Beadle, 1972; Morat & MacKee, 1977). *Trimenia neocaledonica* has invariably been described as having 12 stamens, even in the recent studies of Rodenburg (1971) and Morat and MacKee (1977). In our material it varied from 11 to 15, with an average of 13.2.

Thus, the family Trimeniaceae is an additional one within the Magnoliidae to have spiral floral phyllotaxy (cf., for example, Endress, 1980a, 1980b). In all these cases there tends to be an obvious correlation between spiral phyllotaxy, marked plastochrons, and considerable variation in the number of floral parts.

**PERIANTH.** In the Trimeniaceae, as in other Magnoliidae with spiral floral phyllotaxy, there is neither a separation into perianth members and bracts toward the floral periphery nor a clear differentiation of two different kinds of perianth organs—sepals and petals (see also Hiepko, 1965; Endress, 1980a, 1980b).

**ANDROECIUM.** Stamen structure is unremarkable. The stamens have neither the valvular dehiscence and paired appendages typical of the Laurales nor a massive construction as in many Magnoliales; they are differentiated into filament and anther. The shape of the long, slender anthers and thin filaments of some *Trimenia* species is unusual and resembles that of many wind-pollinated groups in various angiosperm families (e.g., Eupteleaceae; cf. Endress, 1969).

The Trimeniaceae differ from the Chloranthaceae (Vijayaraghavan, 1964), the Lauraceae (Bhandari, 1971), the Monimiaceae (Sampson, 1969a, 1969b; Bhandari, 1971), and most other members of the woody Ranales in having a middle wall layer only one or two cells in thickness. In having a glandular tapetum the Trimeniaceae resemble the Calycanthaceae (Bhandari, 1971), the Chloranthaceae (Vijayaraghavan, 1964), *Cassytha* of the Lauraceae (Sastri, 1963), and the Monimiaceae. This contrasts with other members of the Laura-

TABLE 1. Similarities between four species of Trimeniaceae.

Character	Species			
	<i>Trimenia papuana</i>	<i>T. weinmanniifolia</i>	<i>T. neocaledonica</i>	<i>Piptocalyx moorei</i>
HABIT	Tree			Vine
TEPAL NUMBER	≥ 11			≤ 11
NUCELLAR APEX	Not depressed			Depressed
LEAF MARGINS	Toothed		Entire	
INFLORESCENCE TYPE	Compound botryoids (panicles)		Simple botryoids	
FLOWER BUD SHAPE	Elongate		Globular	
TEPALS				
VASCULARIZATION	One bundle		Bundle branching	
INNERMOST, SHAPE	Spathulate		Obovate	
OUTER, SHAPE	Markedly hypopeltate		Weakly hypopeltate	
ANTHER DEHISCENCE	Latrorse		Extrorse	
POLLEN	Polyforate or inaperturate		Disulculate	

ceae, which have an amoeboid tapetum (Sastri, 1963). Successive cytokinesis, recorded in microspore mother cells of the Trimeniaceae, has also been found in some Monimiaceae (Sastri, 1963; Sampson, 1969a, 1977) and in the Lauraceae (Bhandari, 1971); simultaneous cytokinesis has been found in another member of the Monimiaceae (Sampson, 1969b) and in the Calycanthaceae (Bhandari, 1971) and Chloranthaceae (Vijayaraghavan, 1964). As is characteristic of the more primitive groups of angiosperms (Brewbaker, 1967), the Trimeniaceae shed pollen in the two-celled condition, although three-celled pollen has been found in one genus of the Lauraceae (Gardner, 1974) and in one member of the Monimiaceae (Sampson, 1969b).

**GYNOECIUM AND FRUIT.** The mature carpel is totally utriculate up to the stigma. This was inferred by Leinfellner (1969) from the description of the vasculature in Money, Bailey, and Swamy (1950) and is confirmed in this study. However, the vasculature of the carpel at anthesis is more complicated in *Trimenia papuana* and the two other species investigated than was described by Money, Bailey, and Swamy. Furthermore, they did not report the presence of a vascular bundle in the outer integument.

A remarkable morphogenetic feature is that in spite of the fully utriculate condition of the carpel at anthesis, the early developmental stages are relatively less utriculate and thus more closely resemble those of the Lauraceae and some Monimiaceae (Sampson, 1969a; Endress, 1972, 1980a). The Trimeniaceae are therefore one more example of a family in the Magnoliidae with extremely utriculate carpels (see, for example, Endress, 1980b).

The ovule of the Trimeniaceae has several peculiar lauralian traits that it shares especially with certain Lauraceae, Hernandiaceae, and Calycanthaceae, but (interestingly) less with the Monimiaceae. However, only a few representatives of these families have been studied so far (see TABLE 2, and Endress, 1972), and it is not known how widely distributed these traits are within the Laurales. Such features are the differentiation of many meiocytes in the nucellar base, the marked elongation of the nucellus after meiosis, the apical depression of the nucellus, and the tubelike, intrusive growth of the embryo sac toward

TABLE 2. Occurrence in related families of characters found in the Trimeniaceae.\*

CHARACTER OF TRIMENIACEAE	RELATED FAMILIES			
	Lauraceae	Chloranthaceae	Hernandiaceae	Monimiaceae, s.l.
Climber ( <i>Piptocalyx</i> )	( <i>Cassytha</i> )	—	(+)	( <i>Palmeria</i> )
Leaves opposite	(+)	+	—	+
Node unilacunar, 2-trace	+	+	—	—
Mucilage cells present (L)	+	—	(+)	—
Anemophily	—	(+)	—	( <i>Hedycarya</i> , p.p.?)
Floral phyllotaxy spiral	—	—	—	(+)
Stamen without appendages	—	+	(+)	(+)
Anther dehiscence longitudinal	—	+	—	(+)
Tapetum glandular	( <i>Cassytha</i> )	+	?	+
Pollen meiosis successive	+	—	?	(+)
Pollen inaperturate ( <i>Trimenia</i> , p.p.) (Walker, 1976) (L)	+	(+)	+	+
Exine tectate-columellate (Sampson & Endress, in press; Kubitzki, 1981)	—	+	—	( <i>Laurelia</i> )

Carpel 1 per flower	+	+	+	( <i>Xymalos</i> )
Carpel extremely utriculate at anthesis	-	(+)	-	-
Carpel development including chairlike stage	+	+	?	(Monimioideae)
Ovule 1 per carpel, in ventral-median position (L)	+	+	+	+
Ovule anatropous, pendent (L)	+	-	+	(Monimioideae)
Outer integument with vascular bundle (Van Heel, 1971)	-	-	( <i>Hernandia</i> )	-
Exotesta with palisade-shaped cells (Corner, 1976)	( <i>Cassytha</i> and other genera)	-	-	-
Fruit: berry	(+)	-	-	-
Nucellus elongated (L)	+	-	(+)	-
Nucellar apex depressed ( <i>Piptocalyx</i> )	( <i>Cassytha</i> )	-	( <i>Gyrocarpus</i> )	-
Meiocytes several per ovule (L)	( <i>Cassytha</i> )	-	?	( <i>Siparuna</i> )
Embryo sac narrow, tubular (L)	+	-	+(?)	( <i>Siparuna</i> )
Chromosome number $n = 8$ (Goldblatt, 1974; Goldblatt & Briggs, 1979; Ehrendorfer, 1976; Raven, 1976)	-	( <i>Hedyosmum</i> )	-	-

\*References are not given for characters reviewed in Money, Bailey, and Swamy (1950) and Endress (1972) or discussed elsewhere in this paper.  
Explanation of symbols: L, characteristic "lauralian" feature; +, present; (+), sometimes present; -, absent; ?, unknown.

the nucellar apex (and eventually into the micropyle in other Laurales). These features seem to be less prominent in the Magnoliales.

The fruits of the Trimeniaceae have variously been described as berries (e.g., Rodenburg, 1971) or drupes (e.g., Morat & MacKee, 1977). This may be partly because the term "berry" is not always used in the same sense, but it is also due to misinterpretation of the fruit. The fruit contains a hard layer that is grooved or ridged on the outer surface in some species. Although the hard layer looks like the endocarp of a drupe, it clearly corresponds to the periphery of the seed. The fruit is, therefore, a one-seeded berry.

#### SYSTEMATIC CONCLUSIONS

RELATIONSHIPS WITHIN THE FAMILY. *Trimenia* and *Piptocalyx* were last compared by Gilg and Schlechter (1923). According to their key, *Trimenia* has 15 to 20 spiral tepals, *Piptocalyx* 4 to 6 biseriate ones. The present study has shown that the two genera are less distinctive in these features. Both have spiral tepals, and in rare cases *Piptocalyx* may have as many as 11, therefore reaching the lower limit of the tepal range of *T. papuana*, as given by Rodenburg (1971).

Another surprising result is that *Trimenia neocaledonica* shares some features with *Piptocalyx* that it does not share with the other *Trimenia* species. In particular, the discovery that the pollen of *T. neocaledonica* is disulculate as in *Piptocalyx* (not polyforate or inaperturate as in the other *Trimenia* species) is of interest in this context (Sampson & Endress, in press). Thus, *T. neocaledonica* clearly occupies a central position within the family. This is shown by TABLE 1.

It seems, therefore, that the only obvious differences left between *Trimenia* and *Piptocalyx* are growth form (tree vs. vine) and tepal number ( $\geq 11$  vs.  $\leq 11$ ).

From these results three possibilities for a classificatory consequence arise: the transfer of *Trimenia neocaledonica* to the genus *Piptocalyx*, the merger of *Piptocalyx* with *Trimenia*, or no change. The justification for following any of these three possibilities is about equal. We prefer the third possibility because it avoids unnecessary nomenclatural changes.

On the whole, the Trimeniaceae appear to be a rather uniform family. *Trimenia neocaledonica* is possibly the most primitive species.

RELATIONSHIPS WITH OTHER FAMILIES. Until the classic study on the Monimiaceae by Money, Bailey, and Swamy (1950), *Trimenia* and *Piptocalyx* were usually included in that family. Money, Bailey, and Swamy discussed the reasons for segregating these two genera into a separate family (following Gibbs, 1917) and found relationships with the Lauraceae, *Austrobaileya*, and the Chloranthaceae, in addition to the Monimiaceae. Thorne (1976) pointed to rather close relations with the Chloranthaceae; Takhtajan (1980), with the Amborellaceae. Dahlgren (1980) listed the Trimeniaceae between the Austrobaileyaceae and the Monimiaceae, and Cronquist (1981) placed them between the Amborellaceae and the Monimiaceae.

The results of our study underline the isolated position of the Trimeniaceae. The family shows relationships with the Lauraceae (especially the Cassythoi-



deae), the Chloranthaceae, and the Monimiaceae, but it is only distantly related to the Austrobaileyaceae. The Amborellaceae are still not well enough known for a comparative evaluation. The Hernandiaceae also share a number of special characters with the Trimeniaceae. Those of particular interest are listed in TABLE 2.

That the Trimeniaceae belong to the Laurales is shown by some characteristic "lauralian" features (see TABLE 2). The core of the Laurales consists of the Monimiaceae, Lauraceae, Hernandiaceae, and Gomortegaceae.

However, several characters deviating from those generally found in the Laurales point to the isolated position of the Trimeniaceae. These characters include absence of a floral cup; spiral floral phyllotaxy—also present in Gomortegaceae and some Monimiaceae; caducous tepals; stamens without flaps and appendages—also present in some Monimiaceae; extremely utriculate carpels; polyporate pollen; tectate-columellate exine—also present in *Laurelia*; capitate stigma with multicellular papillae; outer integument with vascular bundle—also present in *Hernandia*; chromosome number of  $n = 8$ . Although the Trimeniaceae share a few of these characters with the Magnoliales, their affinities to the Laurales are still stronger, in spite of their isolation. A closer relationship with the Austrobaileyaceae, as supposed by some authors, can be excluded because the common shared features (vine, leaves opposite, node unilacunar and two-trace, floral phyllotaxy spiral, carpels extremely utriculate, outer integument with vascular bundle) are too scattered. The Austrobaileyaceae are of clearly magnolialian (not lauralian) affinity (Endress, 1980b).

Thus the Trimeniaceae are a very homogeneous, isolated relict family of the Laurales with closest relationships to the Lauraceae, Monimiaceae, Chloranthaceae, and Hernandiaceae; at the same time they are somewhat distant in certain characters from the core of the Laurales.

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